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Key factors that influence breeding performance in raptors

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Introduction

Breeding performance is a broad term, the definition of which varies throughout the literature. In raptor species it is frequently used as an expression that refers to the total number of nestlings that adults can raise to a prescribed age per breeding attempt, however it has also been defined in terms of clutch size, hatching success, and nestling quality (Steenhoff and Newton 2007).

Assessing the breeding performance of raptors (combined with assessment of adult survival rates) is crucial to understanding the health and condition of populations and the degree to which they are likely to persist in a given habitat (Newton 1979; Steenhoff and Newton 2007). Raptors are frequently apex predators in terrestrial habitats, and as a result the study of their breeding success can also be used as a performance based indicator in ecological restoration and monitoring initiatives (Stout et al 2006; Martin et al 2008).

Therefore this review aims to give a comprehensive summary of the theoretical and empirical evidence provided in the literature that has been used to identify the key factors that influence breeding performance in raptors and how these apply to both conservation initiatives and future research.

Age

Numerous avian species have been documented to improve their breeding performance with age, particularly raptors (Forslund and Pärt 1995). As a result, theories have emerged on how raptors (and avian species as a whole) use adaptive life-history strategies in order to influence both their lifetime breeding performance and survival with increasing age.

The 'constraint' theory (Curio 1983) suggests that birds acquire and refine the necessary repertoire of skills required to improve reproductive performance through experience as they age, particularly their ability to forage, incubate, and care for their offspring (Nielsen and Drachmann 2003; Krüger 2005). Therefore it is thought that as individuals improve their proficiency in fundamental skills so to does their breeding performance. In a unique investigation Rutz et al (2006) provide empirical confirmation of this theory in Goshawks (*Accipiter gentilis*). Improvements in both foraging success and capture of prey with greater nutritional value due to age related

experience resulted in direct improvements to nestling growth and survival as parents aged. However it should also be noted that increasingly older age (particularly in individuals held in captivity) has been shown to cause breeding performance to plateau and eventually decrease (despite increasing experience) due to the accumulative effects of senescence (Newton and Rothery 2002; Rebke et al 2010).

Alternatively the 'restraint' theory (Forslund and Pärt 1995) suggests that individuals either abstain entirely or reduce the effort that is invested in breeding in the early years of life in order to accrue physiological stockpiles and avoid the costs to survival that are inherent with reproduction at that age. As the potential for future breeding (residual reproductive value (RRV)) decreases through age then the necessity to breed is presumed to increase in order to maximise lifetime fitness, and as a result breeding performance improves incrementally. Yet as both Forslund and Pärt (1995) and Espie et al (2000) highlight, the ability for studies to prove this theory empirically is exceptionally difficult, particularly when attempting to differentiate between the influence of constraint and restraint in individuals. Therefore Espie et al (2000) produced the 'inadequate experience' theory whereby skill constraints and reproductive restraint are thought to act simultaneously to generate increased breeding performance with age.

Nevertheless, Velando et al (2006) experimentally illustrated that in long lived seabirds aged individuals (with low RRV) which have been immunologically compromised are able to dramatically increase their reproductive output to ensure that breeding performance is maximised. Whereas younger individuals (with high RRV) do not, instead favouring to restrain from breeding in an attempt to ensure both future survival and breeding prospects. These results would suggest that RRV may play a key role in influencing breeding performance of avian species (including raptors). However few studies have been able to highlight the degree to which it may govern breeding performance and as a result there is scope for further investigation in the future, particularly within captive populations.

In addition, Forslund and Pärt (1995) highlight that consistency of phenotypic quality varies throughout populations, and therefore under the 'differential mortality' hypotheses phenotypic quality may also be a principal factor governing breeding performance. Greater phenotypic quality is thought to equate to a genetic predisposition to both improved survival and reproduction in comparison to other phenotypes in any given population. Therefore as weaker phenotypes die off only individuals of higher quality are left in the cohort, giving rise to a proportional increase in reproductive performance with age.

However empirical justifications of this theory, particularly in raptors, also appear rare. Authors such as Blas et al (2009) ascribe the differences in age related breeding performance in Black Kite (*Milvus migrans*) as a combination of both phenotypic quality and experience based improvement as a result of their inability to quantify the influence of either. However more recently Rebke et al (2010) pioneered a formula and methodology that allowed separation of individual change and compositional change at a population level to highlight the level of influence that phenotypic quality has on Common Tern (*Sterna hirundo*) breeding performance. Phenotypic quality was shown to have a low level influence in breeding performance (13%) whilst ontogenetic development (possibly due to improved proficiency in

breeding related skills) accounted for 87% of age related improvements in breeding success. Therefore continued development of population modelling and analytical methodology may well allow authors in the future to reveal the degree to which phenotypic quality and adaptive strategies influence the breeding performance of raptors with age.

Clutch Size

Clutch size is known to have an influence on the breeding performance of many species of birds (Newton 1979). However it is thought that in most avian species it has been adaptively regulated in order to ensure both productivity and survival is maximised throughout their life as part of a cost benefit strategy (Williams 1966). Therefore whilst larger clutches have been shown to be more productive, their cost to parental survival strategy is often cited as being evolutionarily unsuitable (Williams 1966). Instead individuals that produce submaximal clutches are frequently recognised as having better survival prospects and therefore are likely to increase their lifetime breeding performance in comparison to maximal breeders (Charnov and Krebs 1974; Boyce and Perrins 1987). As a result the occurrence of large clutch sizes in wild populations of avian species is far less frequent than clutches of moderate size which promote both breeding performance and survival, as shown by Dijkstra et al (1990) in the Common Kestrel (*Falco tinnunculus*). Furthermore other studies on raptors have suggested that clutch size may also adaptively adjust to varying prey populations in order to optimise lifetime fitness (Olsen and Marples 1992).

Prey Abundance and Accessibility

The ability for parents to provision food to their young and overall prey abundance has often been empirically documented to have a decisive influence on breeding performance in raptors (Newton 1980; Byholm and Kekkonen 2008; Löhmus 2011; McIntyre and Schmidt 2012). Larger prey populations frequently equate to more efficient food provisioning by parents to offspring, improving both survival and growth, and therefore increasing overall breeding performance (Newton 1980). Raptors also utilise prey provisioning from males to females as a courtship mechanism through which females accrue adequate physiological resources to initiate gonadal development, copulation, and egg laying (Newton 1979; Green and Krebs 1995; Amar et al 2003). Therefore prey population levels, and the subsequent ability of parents to capture prey, can influence not only the overall breeding performance of raptors, but also the likelihood that they will breed to begin with.

In recognition of the influence that food has on fitness, a number of theories have emerged to attempt to explain the adaptive strategies employed by raptors to optimise breeding performance under varying levels of food availability as part of a cost benefit strategy (Clutton-Brock 1991). Lack (1954) originally suggested the 'brood reduction hypothesis', an adaptive hedge bet strategy, whereby altricial birds (including the majority of raptors) which incubate their eggs asynchronously do so to develop a chick feeding hierarchy that is adaptive to food abundance and preserves fitness. Plentiful food levels were hypothesised to equate to parents being able to raise the entire brood, with younger chicks surviving but being of comparatively lower quality (in terms of size), to their older counterparts. Whereas diminished food levels were thought to result in the rapid death of younger chicks in an attempt to ensure

that breeding performance (the survival of the remaining offspring) was not entirely compromised.

However despite a slight revision of the original theory by Pijanowski (1992) and support by a number of studies, particularly in raptors (Wiebe and Bortolotti 1994; Green and Krebs 1995), many authors continue to contest the brood reduction hypothesis as the single adaptive basis of hatching asynchrony, with a wide variety of diverse theories arising as a result (Stoleson and Beissinger 1995). Hypothesis on adaptive benefits range from responses to: siblicidal interactions (Edwards and Collopy 1983) reduced breeding opportunities (Beissinger and Waltman 1991) or attempts to reduce predator impact (Konarzewski 1993). However recently authors have begun to suggest that hatching asynchrony arises as a reaction to the sum of selection pressures that are presented to individuals in any one given habitat, and that its occurrence is frequently species or even population specific (Stenning 1996; Viñuela 1999; Padilla and Viñuela 2011). Therefore whilst the exact evolutionary origin is still heavily contested, hatching asynchrony is frequently assumed by many (but not all, see - Hillstrom and Olsson 1994) to be an adaptive evolutionary strategy employed by avian species in order to attempt to ensure that both breeding performance and survival is maximised under a contextual array of selection pressures.

Conversely in a review of the literature concerning owls, Korpimäki (1988) hypothesised high prey abundance may encourage a number of other species of raptors to engage in adaptive polygyny. Greater prey populations (particularly rodents) were hypothesised to enable the male of a breeding pair to initiate a separate clutch with another female, enhancing his own breeding performance whilst the original female capably provisioned the offspring on her own. However despite the fact that recent investigations on Tengmalms owls (*Aegolius funereus*) (Eldegard and Sonerud 2009; Zárybnická 2009; Korpimäki et al 2011) concur with an adaptation of this theory (sequential polygamy), documented cases of other raptors engaging in this behaviour appear rare, possibly due to the inherently monogamous and territorial nature of many other raptors in comparison to that of owls (Newton 1979).

In addition authors have also highlighted that habitat characteristics (such as grass height, and water level) may modify the influence that prey populations have on breeding performance of raptors due to the way in which they alter prey accessibility (Aschwanden et al 2005; Virani and Harper 2009; Martin et al 2008). Arlettaz et al (2010) illustrate that Barn Owl (*Tyto alba*) breeding performance declined in areas with wildflower meadows despite large increases in rodent populations (the owls' principle food source). Whilst the meadows provide ideal habitat for rodents, their dense vegetation led to reduced rodent detection and hunting opportunities for Barn Owls, and as a result breeding performance suffered. Instead the owls favoured grassland that facilitated hunting (and therefore successful breeding) despite diminished prey numbers in comparison to those of the meadows.

Therefore habitat quality in terms of both prey accessibility and abundance is frequently cited as a key influence on determining the success with which many raptors can raise young. As a result authors such as Frey et al (2011) continue to suggest that the improved understanding of raptor exploitation of breeding habitat

and food abundance is likely to improve the efficiency with which conservation initiatives can improve wild raptor breeding performance and preserve valuable habitats in the future.

Rainfall

The frequency of heavy rain fall, has frequently been attributed to causing implications on the breeding performance of raptors in the literature (Dawson and Bortolotti 2003; Morrison et al 2009). Both Penteriani (1997) and Kostrzewa and Kostrzewa (1990) highlight that in Goshawks (*Accipiter gentilis*) nest failures are significantly attributed to the frequency and intensity of rainfall. This is due to the fact that in many raptor species prolific rainfall reduces hunting efficiency by impairing flight and altering prey behaviour, therefore increasing foraging costs and limiting the frequency with which parents can provide food to both their young and themselves (Newton 1979). As both Tjernberg (1983) and Steenhoff et al (1997) highlight, persistent heavy rain can also reduce prey populations and therefore amplify the costs of reproduction in raptors, in some cases causing adults to abandon nests in order to preserve survival at the cost of impaired breeding performance. However as Olsen and Olsen (1992) suggest, the degree to which both hunting efficiency and prey populations are limited by rainfall is frequently species and habitat specific. Therefore increased rainfall may also promote breeding performance through improved prey abundance due to increased habitat productivity, particularly in arid environments (Gargett et al 1995).

In a unique investigation Reed et al (2008) also put forward that persistent heavy rainfall early in the lives of Common Guillemot (*Uria aalge*) can amplify their rate of senescence through the need for continuously augmented energetic investment in metabolism and foraging behaviour. This increased senescence then reduces their ability to reproduce successfully in later years, highlighting that rainfall also has the potential to influence lifetime breeding performance long after it has occurred. As a result it could be argued that this study in addition to the suggestions of earlier authors (Thomas et al 2001; Wichmann et al 2003) may highlight the profound effect with which the increasing regularity of stochastic climatic events due to climate change (as a result of human activity) may have on the breeding performance of raptors in the future.

Human Influence

Many species of raptor have been documented to take advantage of the conditions made available to them due to anthropogenic presence to enhance breeding performance (Herbert and Herbert 1965; Chase and Walsh 2006; Stout et al 2006). Populations of raptors have been studied to undergo forms of synurbanization, a hybridisation of terms used by some authors to broadly describe species which have adapted to an urban environment; utilising tall buildings, urban parks, and gardens as nest sites in favour of rural surroundings, or as a form of 'overflow' when rural territories are fully occupied (Boal and Mannan 1998; Rutz 2008). Urban habitats have frequently been documented to have far lower predator numbers in comparison to those of rural habitats, and therefore the ability for these raptor species to breed and raise young successfully is often presumed to improve as a result (Chipman et al 2008). Whilst in a recent review of the literature Lambrechts et al (In press) also suggests the introduction of artificial nest boxes (both urban and rural) has led to improved breeding performance across a wide range of raptor species due to their

design and location allowing for enhanced food provisioning, and predator avoidance.

Urban environments have also been documented to give rise to inflated and highly stable prey populations, improving breeding performance by allowing enhanced levels of offspring food provisioning and reduced costs to parental fitness (Marches et al 2002). Studies have also begun to suggest a significant adaptive shift in the hunting behaviour of raptors to exploit the unique circumstances present in urban environments. Many species have been documented utilising the artificial light provided in urban habitats to hunt prey nocturnally (and therefore more efficiently), whilst Peregrines (*Falco peregrinus*) have also been observed to heavily exploit migrating birds that collide with buildings and benefit from increased hunting efficiency as a result (Negro et al 2000; Candido and Allen 2006). Additionally Gehlbach (1996) also highlights that many urban environments tend to have mild climates with moderate temperatures and low rainfall that greatly improve the ability of raptors to raise young successfully, particularly during the first week of life when chicks are still developing their thermoregulatory mechanisms.

As a result numerous authors have suggested that urban raptors gain a significant advantage in both breeding performance and survival over their rural counterparts due to the way in which urban environments propagate advantageous ecological conditions for breeding (Gehlbach 1996; Stout et al 2006; Chace and Walsh 2006; Solonen 2008). However caution must also be applied when considering vague inferences made on factors influencing breeding performance such as those by Rejt (2003) concerning urban food abundance and the onset of laying. Whilst studies of this nature (a short study period and small sample size) appear rarely in the literature, they emphasise the necessity for both clear investigation design and the statistical power provided via large data sets employed in other investigations (Steenhof et al 2007; Rutz 2008; Rebke et al 2010) in order to reach constructive, justifiable conclusions on factors that influence breeding performance.

Under certain circumstances urban habitats also present a considerable risk to raptor breeding performance (Hager 2009). Studies by Boal and Mannan (1999) and Krone et al (2005) highlight that nest failures are significantly higher in urban populations of Coopers hawks *Accipiter Cooperii* and Goshawks *Accipiter Gentilis* as a result of trichomoniasis (a parasitic infection of the upper digestive tract) due to higher urban prey populations causing inflated parasitic spread. Whilst Tella et al (1996) also highlight that in populations of Lesser Kestrel (*Falco naumanni*) nestling mortality due to starvation was far greater in urban populations than those in rural habitats, suggesting that not all urban areas benefit from the exaggerated, healthy prey populations documented in other studies.

Furthermore, anthropogenic presence has been shown to have other negative impacts on raptor breeding performance both in urban and rural environments. The alteration of key breeding habitat by humans for agriculture has been to seen reduce raptor breeding performance largely due to the way in which it alters prey abundance in addition to removing trees used for both nesting and hunting (Martínez et al 2008).

Additionally the use of organochlorine pesticides in agricultural environments has been shown to build up in lipid stores of prey animals via trophic transfer causing

reductions in egg shell index (shell thickness) in the raptors which prey upon them (Enderson et al 1982; Newton et al 1986). Subsequently embryo growth in raptor eggs (particularly falcons) contaminated by organochlorines has been documented to be fatally impaired, whilst reductions in structural strength has led to rupture and collapse of eggs during incubation. This was frequently argued to be the leading cause of catastrophic declines in the breeding performance of a number of raptor species during the 1950s and 1960s (Kiff et al 1979; Newton et al 1989) some of which is still observed in a number of current habitats (Helander et al 2002). Similarly the effect of polychlorinated biphenyl pesticides via trophic transfer has been shown to significantly modify the behaviour of raptors through manipulating endocrinal expression; impairing breeding specific behaviours such as courtship, incubation, and food provisioning resulting in reduced reproductive success (Fernie et al 2003).

Human disturbance, particularly through large amounts of repeated human presence (such as construction) close to nests has also been cited as causing the majority of nest failures in some populations of raptors (Holthuijzen 1990). These forms of disturbance often cause adults to abort brooding behaviour leaving young nestlings or eggs exposed to lethal fluctuations in temperature impairing breeding performance as a result (Penteriani et al 2003). Whilst the destruction of nests and nestlings by humans has also been frequently documented to occur when raptors come into conflict with human interests, particularly when they are suspected of preying upon species used in recreational activities (Etheridge et al 1997; Amar et al In Press) or when competition for a primary food source exists between both raptors and humans (Chiweshe 2007).

Therefore human presence, particularly the ability of humans to alter the environments in which they live, has been attributed to significantly altering the breeding performance of raptors. Consequently continued observation via scientific investigation is likely to be required to ensure that anthropogenic presence does not fatally restrict the ability with which raptors can breed successfully in the future.

Conclusion

As this review has highlighted, a wide range of factors have the ability to influence the degree to which raptors can breed successfully in both the short and long term. These factors are frequently complex and often specific to species, populations, and habitats. Subsequently, understanding the systems which drive breeding performance is of crucial significance to conservation organisations which look to preserve and monitor raptor populations. In addition the degree to which these factors influence breeding performance has frequently been argued to be modulated by adaptive evolutionary strategies employed by raptors; yet as this review has illustrated, empirical justification of these theories is frequently scarce.

As a result future studies should look to quantify the complex mechanistic relationships between extrinsic factors and adaptive strategies as well as how they interact to ultimately mould breeding performance in raptors. The continual improvement of analytical models combined with the increasing utilisation of populations held in captivity may provide an ideal environment in which to do so. Such studies may in turn provide specific objectives to conservation initiatives through which they can advise policy makers, facilitate captive breeding, and optimise habitat management.

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